cell dendrites that innervate the glomeruli. Fish granule cells could inhibit transfer of odorant information from the glomeruli to the mitral cells by shunting excitatory currents or by preventing spike conduction along the dendrites. If the sensory information arriving from individual dendrites is differentially controlled by granule cells, mitral cells would be able to receive information from select glomeruli. By altering the timing of granule cell-induced inhibition of individual dendrites, a mitral cell may be activated by different sets of glomerular inputs at different times. Thus, the representation of odorants by an ensemble of mitral cells would change with time, which is just what Friedrich and Laurent describe (*5*). This scenario is reminiscent of that in rabbit retinal ganglion cells that convey information about the directional selectivity of visual stimuli. Arrival of visual information at the dendrites of direction-selective ganglion cells depends on a balance between the excitatory inputs from bipolar cells, which allow signals to pass along the dendrites, and the inhibitory inputs from amacrine cells, which do not (*10*).

What is the advantage of the slow change in response specificity to odorants in zebrafish mitral cells? Working on their zebrafish brain explant with the nose attached, Friedrich and Laurent set up their experiments such that the fish's nose was stimulated over the course of 1 second by a continuous stream of odorants. Their analysis of odorant representations under these conditions led the authors to propose that the slow change in mitral cell responses might afford both a coarse classification of odorants during the initial response phase and a much finer discrimination later on.

Odorants in both water and air, however, typically form a plume that rapidly and continuously changes its shape; thus, an animal's nose encounters odorants intermittently. In their search for food or a mate, fish actively swim around and mammals keenly sniff the air to sample odorants. It is therefore possible that fish mitral cells with multiple glomeruli evolved to respond selectively to the changing patterns of certain odorants in water. Evidence from work by Christensen and Hildebrand (*11*) in the multiglomeruli projection neurons (equivalent to vertebrate mitral cells) of the antennal lobe of male sphinx moths suggests that this might be the case. Single projection neurons send dendrites to two glomeruli within a macroglomerular complex. Each member of the pair of glomeruli receives sensory information from olfactory neurons about one of the two key components of the female sphinx moth sex pheromone. Responses of projection neurons to short repetitive pulses of sex pheromones indicate that the two key components activate opposing synaptic inputs at the two different glomeruli. This enables the multiglomeruli projection neurons to replicate the duration and frequency of intermittent odorant pulses. Frequency coding by these neurons may be important as the male moths fly in a zig zag path, attempting to trace the intermittent plume of female sex pheromone.

Each type of neuron typically has its own characteristic branching pattern of dendrites and receives specific synaptic inputs only on selected parts of the dendritic arbor. How individual neurons integrate information from synapses spread across their broad dendritic tree remains unclear. In the multiglomeruli mitral cells of fish, each dendrite connects with a defined glomerulus, which receives incoming signals from only one type of odorant receptor (see the figure). Thus, fish mitral cells may strategically arrange different odorant receptor inputs on different dendrites, and may introduce a time component to enable switching of the flow of incoming signals from one dendrite to another. The multi-glomeruli mitral cells of zebrafish are an excellent model system with which to explore how individual neurons integrate a multitude of incoming sensory information.

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PERSPECTIVES: COSMOLOGY

In Support of Inflation

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What created the initial inhomogeneities in the universe that resulted in galaxies, clusters of galaxies, and other large-scale structures? This problem continues to puzzle cosmologists. But whatever the mechanism, it must have left its signature in the cosmic microwave background (CMB) radiation (*1*). The CMB is a relic of the Big Bang, a cold bath of light just a few degrees above absolute zero that pervades the entire universe. Released when matter began to become structured, the CMB is our earliest "snapshot" of the universe. Variations (or anisotropies) in its effective temperature tell us about the size and strength of the initial seeds in the primordial plasma, those clouds of gas that clumped together under gravitational attraction and led to the birth of galaxies. Recent CMB experiments suggest that these fundamental seeds could have resulted from tiny quantum fluctuations generated in the early universe during a period of rapid (faster than light) expansion called inflation.

Early on, when the universe was small and very hot, the free electron density was so high that photons could not propagate freely without being scattered by electrons. Ionized matter, electrons, and radiation formed a single fluid, in which the inertia is provided by the baryons (particles that have mass) whereas the photons exert a net outward pressure that halts gravitational collapse. An important property of this fluid was that it supported sound waves. The gravitational clumping of the effective mass was resisted by the restoring radiation pressure, resulting in gravity-driven acoustic oscillations in both fluid density and local velocity.

As the universe expanded and ambient temperatures decreased, high-energy collisions became less and less frequent. The now relatively low-energy photons could not destroy the increasing number of neutral particles (mostly hydrogen) that began to combine. Cosmologists refer to this period as recombination. Soon afterward, the CMB stopped interacting with electrons, making what is called its last scattering upon matter. This is a remarkable event in the history of the universe, because it is the very moment when it passed from being opaque to being transparent to electromagnetic radiation.

Features in the radiation pattern at this time depend on the maximum distance a sound wave could have traveled since the Big Bang. This distance is called the sound horizon. At the time of recombination, the sound horizon was much smaller than it is today (see the bottom figure, next page). To relate the distance between

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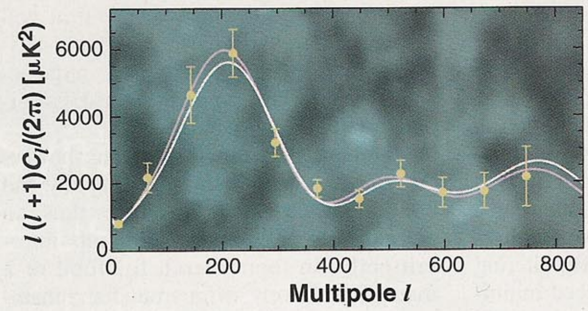
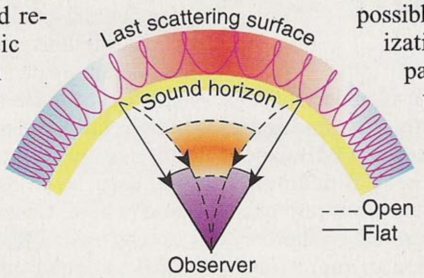
two points at the time of recombination to the equivalent distance observed today, cosmological models use the angle θ between the two points from the observer on Earth (*2*). This relation depends on various unknown cosmological parameters, most importantly the total energy density in the universe. But according to Einstein's general relativity, energy implies curvature. Hence, the curvature of the universe affects the angle θ observed today (see the figure below). Because the sound horizon is a characteristic length in the past, it has a characteristic angle θ on the cosmic microwave background today. For a universe devoid of spatial curvature (a flat or Euclidean geometry), models predict $\theta \approx 1°$. Thus, if the universe were flat, at an angular scale of precisely 1°, we would expect to detect some characteristic feature in the CMB, the "fingerprint" of recombination.

How can this feature be detected? Theoretical model predictions can be compared with observations through the angular power spectrum of the CMB anisotropies. The microwave sky is expanded into a set of functions C_l labeled by the multipole index l, where the lth multipole samples angular scales on the order of $\theta \sim 180°/l$. Hence, C_l gives us the typical strength of the temperature perturbations on that angular scale. A characteristic feature is given by the presence of peaks in the $l(l+1)C_l$ versus l plot. The first acoustic peak is located at the multipole corresponding to the scale of the sound horizon at recombination, when the plasma underwent its first oscillation; it corresponds to a compression mode of the oscillating plasma.

Last year, the BOOMERanG collaboration announced results from the Antarctic long-duration balloon flight mission of 1998 (B98). They found the first peak located at $l \sim 200$, as predicted for a flat universe (*3*, *4*). Only weeks later, the results from another balloon experiment, MAXIMA, were made available on the Internet (*5*, *6*). MAXIMA produced high-resolution maps of a 100-square-degree patch of the northern sky and went beyond B98 in exploring multipoles from $l \cong 36$ to 785, the largest range reported to date with a single experiment.



Distant murmurs. The graph shows combined COBE/DMR, BOOMERanG-98, and MAXIMA results for the CMB angular spectrum. The curves show the best fit model from joint parameter estimation (pink line) and the same for a flat universe (white line). The flat universe fit becomes the best fit when Supernova Ia data are incorporated into the analysis, implying the existence of both nonbaryonic dark matter and dark energy in the universe. Background: part of the MAXIMA-1 map of CMB anisotropy (darkest shade, –300 μK; lightest shade, 300 μK). [Graph adapted from Jaffe *et al.*]



Gazing into the past. The angle observed on the sky today for the sound horizon at recombination depends on the various cosmological parameters. In particular, the spatial curvature of the universe will change the angle under which any feature (like the sound horizon) is seen. [Adapted from a figure by Hu (*17*).]

Recently, a joint analysis of the Cosmic Background Explorer/Differential Microwave Radiometer (COBE/DMR) (*7*), B98, and MAXIMA data sets was published (*8*). The COBE data provide information at low l, necessary for normalization purposes. After correcting for calibration uncertainties, the B98 and MAXIMA data were quite consistent. The experiments used different observation strategies and produced independent power spectra from regions of the sky roughly 90° apart and on opposite sides of the galactic plane. Their consistency gives confidence in the results (see the figure, above).

The presence of a localized and narrow ($\Delta l/l \sim 1$) peak at $l \sim 200$ is in agreement with a flat universe and favors an inflationary model with initial adiabatic perturbations (where fluctuations in all species are correlated). In the absence of a possible later period of reionization, which could erase partly or even completely the acoustic peaks, the physics of recombination predicts the existence of other peaks; the second one corresponds to a rarefaction mode (the opposite of the compression mode) and its characteristic scale is half that of the first peak. In the figure above, we can see a hint of a second peak at $l \sim 500$, but nothing conclusive can be said yet.

Alternative models cannot reproduce these observations. Cosmic topological defects, such as cosmic strings and textures, which are concentrations of primordial energy issued from early cosmological phase transitions, can produce structure in the universe, but cannot fit the present data (*9*, *10*). The complicated nonlinear evolution of these networks continuously perturbs the radiation background all along the photon's journey in an incoherent fashion, leaving as its sole characteristic signature a broad hump and virtually no acoustic peaks (*11*). Recent computer simulations with a cosmic string model (*12*) have failed to generate the CMB variations observed by B98 and MAXIMA on scales below 1°.

The accurate locations and amplitudes of the expected secondary peaks will allow the determination of many fundamental cosmological parameters, such as a possible cosmological constant or other forms of dark energy, such as quintessence (*13*). Full analysis of the B98 and MAXIMA data sets will provide further insights, but conclusive results will require inclusion of CMB polarization data (*14*) and full-sky coverage from the forthcoming satellite-based mission MAP (Microwave Anisotropy Probe) (*15*). Other astrophysical input, such as supernovae and large-scale structure data, in combination with the CMB, has proven successful for removing degeneracies in the determination of fundamental parameters and will be even more important in the future.

The increasing precision of today's detectors demands theoretical modeling to be highly accurate. The CMB contains a wealth of information on cosmology, and future experiments will test our models of structure formation to the limit.

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